

Do the Antillean species of *Gochnatia* KUNTH (Asteraceae) truly belong in that genus? A phylogenetic analysis based on morphological characters

IRALYS VENTOSA RODRÍGUEZ¹ & PEDRO PABLO HERRERA OLIVER²

¹Pasaje El Astillero No. 8
(4401) Vaqueros, Salta, Argentina
iralysv@gmail.com

²National Center for Biodiversity, Institute of Ecology and Systematics
Carretera Varona Km 3½, Capdevila, Boyeros, A.P. 8029
C.P.10800, Ciudad de la Habana, Cuba

Abstract

A phylogenetic analysis was carried out on the species of the section *Anastraphioides* JERVIS ex L. KATINAS, S. FREIRE & G. SANCHO of the genus *Gochnatia* KUNTH, along with representatives of the four genera of the subfamily Gochnatioideae: *Richterago* KUNTH, *Cyclolepis* D. DON, *Cnicothamnus* GRISEB. and *Gochnatia* KUNTH (other sections). The analysis, based on a data matrix of 42 species and 37 morphological, anatomical, and palynological characters, employed TNT (Tree Analysis Using New Technology) version 1.1 (GOLOBOFF et al. 2003). Results showed that the section *Anastraphioides* is a monophyletic, derived group more closely related to *Richterago* than to other sections of *Gochnatia* as currently defined. The species currently in the section *Anastraphioides* of the genus *Gochnatia* present a number of unique characters, suggesting the necessity of taxonomic changes for this group.

Introduction

Since its description in 1819, the genus *Gochnatia* KUNTH (Asteraceae) has generated controversy with respect to its infrageneric classification. Currently it pertains to the tribe Gochnatieae (BENTH. & HOOK. f.) PANERO & V. A. FUNK of the subfamily Gochnatioideae (BENTH. & HOOK. f.) PANERO & V. A. FUNK, along with the genera *Cyclolepis* D. DON, *Cnicothamnus* GRISEB., and *Richterago* KUNTH (PANERO & FUNK 2008), but historically it was placed in the tribe Mutisieae

(KATINAS et al. 2008). The genus is characterized by discoid or radiate capitula with tubular or sub-bilabiate flowers, caudate anthers with apiculate appendages, and glabrous style branches (LESSING 1830, DE CANDOLLE 1836, CABRERA 1971). During its taxonomic history the genus *Gochnatia* has at various times been thought to include other genera such as *Leucomeris* D. DON, *Anastraphia* D. DON, subgen. *Hedraiophyllum* LESS., *Pentaphorus* D. DON, and *Moquinia* DC. This lack of agreement has led several authors to consider *Gochnatia* as an artificial taxon whose clarification is of considerable importance to understanding phylogenetic relationships within the family Asteraceae (CABRERA 1971, BREMER 1994, FREIRE et al. 2002).

The exhaustive infrageneric treatment by JERVIS (1954) recognized five sections in the genus: *Anastraphioides* JERVIS ex L. KATINAS, S. FREIRE & G. SANCHEZ, *Gochnatia*, *Hedraiophyllum* (LESS.) DC., *Pentaphorus* (D. DON) LESS., and *Moquinia* (DC.) JERVIS. His work listed 71 species and considered the species formerly included in a separate genus, *Anastraphia*, as the section *Anastraphioides*. In his monograph of the genus, CABRERA (1971) included the species of *Anastraphioides* within the section *Gochnatia* LESS. and recognized five other sections: *Pentaphorus* (D. DON) DC., *Moquiniastrium* CABRERA, *Leucomeris* (D. DON) CABRERA, *Hedraiophyllum* (LESS.) DC. and *Discoseris* (ENDL.) CABRERA, the last section comprising the discoid species of the former genus *Seris* LESS.

ROQUE & PIRANI (2001) redefined the genus *Richtera* KUNTH to include the species formerly in *Actinoseris* (ENDL.) CABRERA and the section *Discoseris* of *Gochnatia*, based on analyses of morphological, anatomical and pollen characters of these species (ROQUE & SILVESTRE-CAPELATO 2001, ROQUE 2001). Soon afterwards, FREIRE et al. (2002) published an exhaustive morphological analysis of the species of *Gochnatia* as defined in CABRERA'S (1971) treatment. Among the eight sections redefined by FREIRE et al. (2002) was once again the section *Anastraphioides*, re-established for the Antillean species of *Gochnatia* as defined by JERVIS (1954). The other sections in the treatment of FREIRE et al. (2002) were *Gochnatia*, *Hedraiophyllum*, *Leucomeris*, *Pentaphorus*, *Glomerata*, *Rotundifolia* and *Discoseris*.

More recent studies have recognized *Pentaphorus* and *Leucomeris* as genera independent of *Gochnatia* (HIND 2007). Molecular phylogenies have shown *Richtera* sensu ROQUE & PIRANI (2001) to be related to *Cnicothamnus* GRISEB., *Gochnatia*, and *Cyclolepis* D. DON in the subfamily *Gochnatioideae* (PANERO & FUNK 2002, 2008). Authors such as KATINAS et al. (2008) and SANCHEZ & FREIRE (2009), however, dispute these criteria. Clearly the genus *Gochnatia* still requires a thorough taxonomic revision.

In this vein, the objective of the present study is the phylogenetic analysis of

the Antillean species of *Gochnatia* (sect. *Anastraphioides*), including in the analysis representatives of the sections *Discoseris*, *Glomerata*, *Gochnatia*, *Hedraiophyllum*, *Leucomeris*, *Pentaphorus*, *Rotundifolia* as well as representatives of the genera *Richterago*, *Nicothamnus* and *Cyclolepis*. Based on morphological, anatomical and palynological characters, the analysis is intended to elucidate the taxonomic problems of *Gochnatia*, at least as far as species that make up the section *Anastraphioides* and are endemic to the Greater Antilles and the Bahamas.

Materials and Methods

Selection of species

The analysis included representatives of the four genera of the subfamily Gochnatioideae: *Nicothamnus* (1 species), *Cyclolepis* (1 species), *Gochnatia* (39 species), and *Richterago* (1 species). Following the definition of sections proposed by FREIRE et al. (2002), the genus *Richterago* was analyzed excluding species of the section *Discoseris* of *Gochnatia* (*Gochnatia amplexifolia* and *G. discoidea*) even though some authors place *Discoseris* in *Richterago*, following the definition of ROQUE & PIRANÍ (2001). For *Gochnatia*, representatives were included from all the eight sections defined by FREIRE et al. (2002). For the majority of these sections, the analysis included the type species and whenever possible other species as well. For the section *Leucomeris* as defined by FREIRE et al. (2002), however, the type species (*G. spectabilis*) was not analyzed; the phylogenetic studies of PANERO & FUNK (2008) show that this species pertains to the genus *Leucomeris*, which is not included in the tribe *Gochnatieae* nor even the subfamily Gochnatioideae. Following this reasoning, the section *Leucomeris* needs to be redefined. From this point on we will refer to it as the section aff. *Leucomeris*. Finally, *Cyclolepis genistioides* was selected as the outgroup, based on the results of PANERO & FUNK (2008).

The material examined and analyzed was obtained from the herbaria B, GH, HAC, HAJB, LP, MO, NY, and S, following the acronyms proposed by HOLMGREN et al. (1990).

Selection of characters

The cladistic analysis of the 42 taxa was based on morphological, anatomical and palynological characters that were selected following an extensive review of character variation. Highly variable characters and characters difficult to delimit were excluded. In total the analysis included 37 characters (Table 1).

Table 1. Character states used in the phylogenetic analysis of *Gochnatia* and representative species of *Cnicothamnus*, *Cyclolepis* and *Richterago* of the subfamily Gochnatioideae.

1.	Habit: 0–trees; 1–shrubs; 2–herbs
2.	Presence of brachyblast: 0–absent; 1–present
3.	Position of leaves on branches: 0–grouped towards branch tip; 1–dispersed along the branch
4.	Leaf size: 0–leptophyllous or nanophyllous (<0.25 cm ² or 0.25–2.25 cm ² respectively); 1–microphyllous (2.25–20.25 cm ²); 2–nothophyllous (20.25–45 cm ²); 3–mesophyllous (45–182.25 cm ²)
5.	Presence of spine at leaf tip: 0–absent; 1–present
6.	Leaf texture: 0–chartaceous; 1–coriaceous
7.	Leaf margin: 0–entire; 1–denticulate without spines; 2–spinose–dentate
8.	Non-glandular hairs on leaves: 0–absent; 1–flagellate septate; 2–biramous
9.	Leaf venation: 0–pinnate; 1–three–nerved
10.	Presence of abaxial epidermis of the leaf getting into the mesophyll: 0–absent; 1–present
11.	Presence of sclerenchyme bands in the mesophyll: 0–absent; 1–present
12.	Number of layers in hypodermis: 0– no layer; 1–one layer; 2–two or more layers
13.	Capitulum type: 0– heterogamous; 1–homogamous
14.	Shape of involucre: 0–wide campanulate; 1–campanulate; 2–turbinate
15.	Size of involucre: 0– < 10 mm; 1–10–30 mm; 2– > 30 mm
16.	Presence of attenuated involucre base: 0– present; 1– absent
17.	Position of anthers with respect to corolla: 0–exserted; 1–not exserted
18.	Degree of grouping of capitula (capitulescence): 0–solitary; 1–pseudocorymb; 2–pseudoraceme
19.	Floral peduncles and bracts: 0–absent; 1–peduncle without bracts; 2–peduncle with bracts
20.	Corolla type: 0–isomorphic; 1–subdimorphic; 2–dimorphic
21.	Number of capitula per capitulescence: 0–one (or two–three); 1–few (5–20); 2–many (> 20)
22.	Number of flowers per capitulum: 0–few (<10), 1–many (11–20); 2–numerous (>30)

23.	Number of series of involuclral bracts: 0–up to 4 series; 1–between 5 and 8 series; 2→ 8 series
24.	Texture of involuclral bracts: 0–glabrous; 1–pubescent
25.	Pubescence of involuclral bracts: 0–chartaceous; 1–subcoriaceous
26.	Length of corolla lobes: 0–scarcely lobed; 1–lobes of same length as corolla tube; 2–deeply lobed
27.	Presence of leaf petioles: 0–absent; 1–present
28.	Shape of corolla lobes: 0–erect; 1–recurved
29.	Papillae and hairs at tips of corolla lobes: 0–absent; 1–papillae only; 2–hairs only; 3–papillae and hairs
30.	Form of anther tail: 0–smooth; 1–short laciniate; 2–long laciniate
31.	Pappus type: 0–type A; 1–type B; 2–type C; 3–type D; 4–type E as defined by FREIRE et al. (2002)
32.	Number of series of pappus bristles: 0–one series; 1–two series; 2–three or more series
33.	Grouping of pappus bristles: 0–free; 1–grouped at the base
34.	Surface of pollen grain: 0–echinate; 1–microechinate
35.	Type of exine: 0– <i>Mutisia</i> ; 1– <i>Wunderlichia</i>
36.	Form of anther apical appendage: 0–abruptly acuminate; 1–acute or attenuate
37.	Reproductive system: 0–monoecious; 1–dioecious, polygamous

Characters 10, 11, 12 and 35 were codified as “?” for *Gochnatia arborescens*, where those characters could not be determined from the materials available. Likewise, character 30 was codified “?” for *G. oviedoae* and *G. cristalensis*, and character 35 for *G. wilsonii*, *G. microcephala*, *G. picardae*, *G. oligantha*, *G. enantha* and *G. curviflora*. For the last species, character 34 as well could not be determined (Table 2).

Autapomorphies were not included in the cladistic analysis. The data matrix (Table 2) was analyzed with TNT (Tree Analysis Using New Technology) version 1.1 (GOLOBOFF et al. 2003). All analyses were based on a heuristic search with 1,000 random, additive repetitions (RAS), saving up to 10 trees before running the algorithm “bisection-reconnection” (TBR). Bootstrap methods with 1000 replicates (FELSENSTEIN 1985) were used to evaluate the degree of support for branching patterns. The program Winclade version 0.9.9+ (BETA) was used to analyze homologies and homoplasies (NIXON 1999).

Table 2. Data matrix used in the cladistic analysis of *Gochmatia* and related genera of Gochnatioideae, using the morphological, anatomical and palynological characters defined in Table 1. In all 42 species were evaluated, with *Cyclolepis genistioides* as the outgroup. “?”= signifies missing data (see text).

Species	Characters																																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37			
<i>Cinchonanthus borealis</i>	0	1	0	1	3	0	0	1	0	0	1	0	1	0	2	1	1	0	0	1	1	0	2	1	0	1	0	2	1	1	3	0	3	1	0	0	0	1	0	
<i>Cyclotrips genistioides</i>	1	0	1	0	1	0	2	1	0	0	0	1	0	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	2	4	1	0	1	0	0	1	
<i>Gochmatia</i>	1	0	1	0	1	2	1	0	1	1	1	1	0	1	0	1	1	0	0	0	0	2	1	0	1	1	1	1	1	1	3	0	0	1	1	1	0	0	0	
<i>alt recurva</i>	2	0	1	2	1	0	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	2	2	1	0	1	1	1	1	1	0	2	1	0	1	1	0	0	0	
<i>G. amplifolia</i>	0	0	1	1	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>G. arbuscula</i>	0	0	1	1	1	0	0	1	1	?	?	?	0/1	1	0	1	0	1	1	1	1	2	1	0	1	0	1	0	1	0	0	1	0	0	1	?	1	0	0	
<i>G. argentea</i>	1	0	1	0	1	1	2	1	0	0	1	1	1	1	1	1	0	0	0	0	0	2	2	0	1	0	1	0	1	0	3	1	0	0	0	1	0	0	0	
<i>G. attenuata</i>	1	0	1	0	1	1	2	1	0	0	1	1	1	1	1	2	0	0	0	0	0	0	0	2	0	1	0	1	0	1	2	1	0	0	0	0	1	0	0	0
<i>G. buxifolia</i>	1	0	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	2	0	1	0	1	2	1	0	3	0	0	0	0	1	0	0	0	
<i>G. calceola</i>	1	0	0	1	1	2	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	2	0	1	0	1	2	1	0	1	0	0	0	0	1	0	0	0	
<i>G. coveillei</i>	1	0	0	1	1	2	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	2	1	0	1	0	1	1	1	0	1	3	0	0	0	1	1	0	0	
<i>G. crossifolia</i>	1	0	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	2	1	0	1	0	1	1	1	0	1	2	0	0	1	1	0	0	
<i>G. cubensis</i>	1	0	1	0	1	2	1	0	1	1	1	1	1	1	2	1	1	0	0	0	0	1	0	1	0	1	0	1	1	0	1	0	0	0	1	1	0	0	0	
<i>G. curviflora</i>	2	0	1	2	1	0	0	1	0	0	1	0	1	1	1	1	1	1	0	1	1	0	1	0	1	0	1	1	0	1	0	2	1	1	0	0	2	1	0	
<i>G. discoides</i>	0	0	1	2	1	0	0	1	0	0	1	0	1	1	1	1	1	1	0	0	1	2	1	0	1	0	1	0	1	1	0	2	1	0	0	0	1	0	0	
<i>G. elmanii</i>	1	0	1	1	0	2	1	0	1	0	1	2	1	1	1	1	1	0	0	0	0	2	2	0	1	1	0	1	1	0	1	0	2	1	0	0	1	0	0	
<i>G. elliptica</i>	0	0	1	0	1	0	1	0	1	0	1	2	1	1	1	1	1	0	0	0	0	0	2	0	1	2	1	0	1	1	0	3	1	0	0	0	1	0	0	
<i>G. ellipticameris</i>	0	0	1	0	1	0	1	0	1	0	1	2	1	1	1	1	1	0	0	0	0	0	2	0	1	2	1	0	1	1	0	3	1	0	0	0	1	0	0	
<i>G. encanthera</i>	0	0	1	0	1	2	1	0	1	1	1	2	1	1	1	1	1	0	0	0	0	0	2	0	1	2	1	0	1	1	0	3	1	0	0	0	1	0	0	
<i>G. foliosa</i>	1	0	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	2	0	1	0	1	2	1	0	1	0	3	1	0	0	0	1	0	0
<i>G. glabrata</i>	1	0	1	0	0	0	1	0	0	0	1	0	1	1	1	1	1	1	2	1	1	1	0	0	1	0	1	0	1	1	0	1	3	1	0	1	0	0	0	
<i>G. glabrata</i>	1	0	1	0	0	0	1	0	0	0	1	0	0	1	1	1	1	1	2	1	1	1	0	0	1	0	1	0	1	1	0	1	3	1	0	1	0	0	0	
<i>G. gonczii</i>	1	1	0	1	1	2	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	
<i>G. ilicifolia</i>	0	0	1	0	1	1	1	0	1	0	1	2	1	1	1	1	1	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	2	1	0	1	0	0	0	
<i>G. intertexta</i>	1	0	1	0	1	1	2	1	0	1	0	1	0	1	1	1	1	0	0	0	0	0	1	0	1	0	1	2	1	0	1	0	3	0	0	0	1	0	0	
<i>G. montana</i>	1	0	1	0	1	1	2	1	0	1	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1	2	1	0	1	0	3	0	0	0	0	1	0	0	
<i>G. montana</i>	1	0	1	0	1	1	2	1	0	1	0	1	1	1	1	1	1	0	0	0	0	2	1	0	1	0	1	2	1	0	1	0	3	1	0	0	0	1	0	
<i>G. montana</i>	1	0	1	0	1	1	2	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	1	0	1	0	1	1	0	1	0	2	1	0	0	0	1	0	0	
<i>G. obtusifolia</i>	1	0	1	0	1	0	1	1	0	1	1	0	1	0	1	1	1	0	0	0	0	0	1	0	1	0	1	1	0	1	0	1	0	3	1	0	0	1	0	0
<i>G. obtusifolia</i>	1	0	1	0	1	1	2	1	0	1	0	1	0	1	1	1	1	0	0	0	0	1	1	0	1	0	1	1	0	1	0	2	1	0	0	1	1	0	0	
<i>G. obtusifolia</i>	1	0	1	1	0	1	0	2	0	0	1	0	0/1	1	0	1	1	1	0	1	1	1	1	0	1	0	1	1	0	1	1	2	1	0	2	1	0	0	0	
<i>G. patens</i>	0	0	1	0	1	0	1	1	0	0	0	0	0/1	1	0	1	1	1	2	1	1	1	0	1	0	1	0	1	1	0	1	1	2	1	0	1	0	0	0	
<i>G. patens</i>	0	0	1	0	1	0	1	1	0	0	0	0	0	0	1	0	1	0	2	0	0	0	1	0	1	0	1	0	1	0	1	1	2	1	0	0	1	0	0	
<i>G. parvifolia</i>	1	0	0	0	1	1	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	3	1	0	0	0	1	0	0	
<i>G. parvifolia</i>	1	0	0	1	1	2	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	2	0	1	0	1	0	1	0	1	0	3	1	0	0	0	1	0	0
<i>G. parvifolia</i>	0	0	1	1	1	1	0	1	0	1	1	2	1	1	1	1	1	0	0	0	0	0	2	0	1	0	1	0	1	0	1	0	3	1	0	0	0	1	0	0
<i>G. recurva</i>	1	0	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	0	0	0	0	2	1	0	0	0	1	0	1	0	1	0	3	1	0	0	1	0	0	
<i>G. recurva</i>	1	0	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1	0	0	0	0	2	1	0	0	0	1	0	1	0	1	3	2	1	0	0	1	0	0	
<i>G. rotundifolia</i>	1	0	1	0	1	0	1	0	1	0	1	1	1	1	1	1	1	0	0	0	0	2	1	0	0	0	1	0	1	0	1	3	2	1	0	0	1	0	0	
<i>G. sagittata</i>	1	0	1	0	1	1	2	1	0	1	1	2	1	1	1	1	1	0	0	0	0	2	1	0	1	1	1	1	0	1	0	3	1	0	0	1	1	0	0	
<i>G. shufleri</i>	1	0	1	0	1	1	2	1	0	1	1	1	1	1	1	1	1	0	0	0	0	2	1	0	1	1	1	1	0	1	0	3	1	0	0	1	1	0	0	
<i>G. venenoides</i>	1	0	1	0	1	0	1	0	1	0	1	0	1	1	1	1	1	0	0	0	0	2	1	0	1	0	1	1	0	1	0	3	1	0	0	1	1	0	0	
<i>G. wilsonii</i>	1	0	1	0	1	0	2	1	0	1	0	1	0	1	1	1	1	0	0	0	0	2	1	0	1	0	1	1	0	1	0	3	1	0	0	1	1	0	0	
<i>Rhynchospora unguiculata</i>	2	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	2	0	2	1	0	1	2	0	0	0	3	2	0	0	0	0	0	0		

Results and Discussions

Analyses of the data matrix of 37 characters and 42 taxa (Table 2) provided 24 most parsimonious trees (MPT) with a length of 201 steps, a consistency index (CI) of 0.28, and a retention index (RI) of 0.60. The strict consensus included twelve collapsed nodes. Bootstrap values were low for the majority of the branchings.

The topology of the strict consensus tree demonstrates that the genus *Gochnatia* is not monophyletic when all eight sections defined by FREIRE et al. (2002) are included. The sections themselves, however, largely remain intact, which suggests independent monophyletic origins for the majority of them in spite of the low bootstrap values (Fig. 1). The strict consensus tree reveals a clade formed by *G. argentina* and *G. orbiculata*, closely related species with BS = 84% (Fig. 1). These species represent the monophyletic section *Hedraiophyllum*, sister group to the large clade that includes the remaining species analyzed. In turn, the second clade is a polytomy between *Gochnatia palosanto* and *G. arborescens*, pertaining to the sections aff. *Leucomeris* and *Glomerata* respectively; the clade representing the section *Pentaphorus*; and a third clade uniting the sections *Rotundifolia*, *Gochnatia*, *Discoseris*, and *Anastraphioides* along with the representatives of *Richterago* and *Cnicothamnus* (Fig. 1).

Because only one species each of the sections aff. *Leucomeris* and *Glomerata* was available for analysis, the monophyly of these sections could not be assessed in this study. Still, the tree reveals independence between these two and the remaining sections of the genus even though the precise relationships are obscured by the polytomy. *Gochnatia foliosa* and *G. glutinosa*, the only two species in the section *Pentaphorus*, are defined as a monophyletic group related to the sections *Glomerata* and aff. *Leucomeris*. Bootstrap values for this clade are lower than 50% (Fig. 1).

Next in order in the cladogram is *G. curvifolia* as the basal species as well as the sister species of the remaining taxa. This species plus *G. vernonioides* make up the sister group of the polytomy that includes *G. rotundifolia* (the only species of the section *Rotundifolia*), *Cnicothamnus lorentzii*, the subclade of *Richterago* including the section *Discoseris* (Fig. 1), and the subclade of the section *Anastraphioides* (Fig. 1). For the section *Gochnatia*, *Gochnatia curvifolia* and *G. vernonioides*, the only representatives analyzed, indicate that this section is paraphyletic. A more thorough study that includes the remaining five species of the section *Gochnatia* is needed, however, to establish this beyond doubt.

The analysis shows that *Richterago angustifolia*, *Gochnatia amplexifolia* and *G. discoidea* (section *Discoseris*) constitute a monophyletic group (Fig. 1). This result supports the classification by ROQUE & PIRANI (2001), who placed the species of the

section *Discoseris* in *Richterago*. The subclade of *R. angustifolia*, *G. amplexifolia* and *G. discoidea* as a whole represents the sister group of the subclade containing all the Antillean species of *Gochnatia* (section *Anastraphioides*) (Fig. 1).

The section *Anastraphioides* constitutes a derived and monophyletic taxon. The species divide into two groups (Fig. 1). In the first, with 13 taxa, *Gochnatia maisiana* and *G. maisiana* var. *parviflora* make up the sister group of the remaining eleven species. Next in sequence is *G. buchii*, sister species of the polytomy consisting of *G. intertexta*, the subgroup *G. gomezii*, *G. calcicola* and *G. cubensis*, and the subgroup *G. oligantha*, *G. parvifolia*, *G. wilsonii*, *G. pauciflorescens*, *G. microcephala*, and *G. eneantha* (Fig. 1). The last subgroup of six species is also a polytomy in which *G. parvifolia* and *G. oligantha* are distinct from the remaining four species. The second group, of 15 taxa (Fig. 1), comes out of the analysis as a notable polytomy between five species (*G. attenuata*, *G. ekmanii*, *G. mantuensis*, *G. shaferi*, *G. recurva*) and four subgroups, all of which display low BS values (Fig. 1).

Analysis of the principal characters contributing to the relationships between the sections of *Gochnatia* and related genera

Fig. 2 shows one of the 24 cladograms produced by the analysis and specifies the characters for each of the cladogram branches.

The grouping of species into the section *Hedraiophyllum* is strongly supported by the exclusive synapomorphy of the presence of pappus bristles of equal width but variable length, with plumes at the tip of the longest bristles (pappus type C, character 31, state 2). Other characters that support this grouping are homoplasies such as the presence of sclerenchyme bands in the mesophyll [character 11(1)], slightly recurved corolla lobes [character 28(1)], and pubescent involucre bracts [character 25(1)] (Fig. 2).

Although the grouping of species into the section *Pentaphorus* (Fig. 2) lacks exclusive synapomorphies, the set of characters as a whole supports the grouping. These include flowers with corolla lobes the same length as corolla tubes [character 26(1)], short laciniate anther tails [character 30(1)], and Type D pappus [character 31(3)], the last character a parallelism shared with *Cnicothamnus lorentzii*.

Each of the two sections *Glomerata* and aff. *Leucomeris* is defined by a set of characters constituting synapomorphies. For example, *Glomerata* has numerous series of involucre bracts on the capitulum [character 23(2)], acute or attenuated anther apical appendages [character 36(1)], and smooth anther tails [character 30(0)] (Fig. 2). The section aff. *Leucomeris* is differentiated by denticulate leaf margins [character 7(1)], capitulum with attenuated involucre base [character 16(0)], and capitulum with bracteate floral peduncles [character 19(2)] (Fig. 2).

Despite appearing on different branches, the species currently making up the section *Gochnatia* differ as a group from *Richterago*, *Cnicothamnus*, and the sections *Discoseris*, *Rotundifolia*, and *Anastraphioides* as follows: three-nerved venation [character 9(1)]; one or a few capitula, whose peduncles also lack bracts [character 19(1)]; flowers where papillae appear only on the tips of the petals [character 29 (1)]; pollen grains with echinate exine surface [character 34(0)]; and achenes with pappus bristles of uniform width but variable length (type B) [character 31(1)] and in two series [character 32(1)] (Fig. 2).

Richterago angustifolia and the species of *Discoseris* share the following characters with the section *Anastraphioides*: pappus bristles of uniform width and length (Type A), unique among the species of *Gochnatieae* [character 31(0)] and principally in a single series [character 32(0)]; and spiny leaf tips [character 5(1)] (Fig. 2). *Richterago* (including *Discoseris*), however, differs from *Anastraphioides* in the following ways: exclusively herbs or subshrubs [character 1(2)]; leaves primarily nothophyllous [character 4(2)] and sessile (without petioles) [character 27(0)]; capitula grouped in pseudocorymbs [character 18(1)] but with few flowers each [character 21(0)]; and floral peduncles without bracts [character 19(1)] (Fig. 2).

The section *Anastraphioides* is defined by the presence of coriaceous leaves [character 6(1)] with spinose-dentate margins [character 7(2)] and short lacinate anther tails [character 30(1)] (Fig. 2). Other characters that contribute to the definition of this clade are involucre with more than eight series of bracts [character 23(2)], exine surface microechinate [character 34(1)], and leaf hypodermis with more than two cell layers [character 12(2)]. This section divides into two subclades, as discussed above. One is characterized by turbinate involucre [character 14(2)] as an exclusive character, with few flowers per capitulum [character 22(0)], while the other is characterized by monostratified hypodermis in the leaf mesophyll [character 12(1)] and pollen grains with exine surface microechinate [character 34(1)] (Fig. 2).

Taxonomic considerations suggested by the phylogenetic analysis

The results of this study suggest that the current concept of *Gochnatia*, consisting of the eight sections defined by FREIRE et al. (2002), is actually a paraphyletic group. Most of the individual sections themselves, however, appear to be monophyletic, especially the sections *Discoseris*, *Rotundifolia* and *Pentaphorus* – of which 100% of the species were included in our study – and *Anastraphioides*, of which all species were included except *G. tortuensis*.

The species of the section *Hedraiophyllum* analyzed appear as sister species of *Cyclolepis* (Fig. 1). These *Hedraiophyllum* species constitute a natural group clearly separate from all other sections of *Gochnatia* by reason of subzygomorphic

corollas, functionally feminine flowers, and the pappus with half the bristles long with plumose tips and the other half short (type C). Furthermore, these are the only species currently in *Gochnatia* that have biramous T-shaped hairs (SANCHO 2000, FREIRE et al. 2002). These characters and the closer relation with *Cyclolepis genistioides* than with the representatives of other *Gochnatia* sections indicate that the taxonomic status of this section should be reanalyzed, one possible result being the recognition of a new genus related to but independent of *Gochnatia*.

The representatives of the section *Pentaphorus* also constitute a monophyletic group, sister to the majority of the species currently in *Gochnatia* (Fig. 1). These results coincide with HIND's (2007) recognition of *Pentaphorus* as a genus apart, distinguished by the presence of linear, glandulate-punctate leaves, inflorescences in dense glomerules or pseudoracemes, and pappus bristles of variable length and width (type D).

The section *Discoseris* and the species *Richterago angustifolia* appear as a monophyletic group in the analysis (Fig. 1), coinciding with results of the molecular analysis of PANERO & FUNK (2008). These results also support the classification of ROQUE & PIRANI (2001), but fail to support the classification of CABRERA (1971) often followed by other authors (e.g., FREIRE et al. 2002, SANCHO et al. 2005). Our study supports the concept of the monophyletic genus *Richterago*, characterized by herbaceous or subshrub growth form, scapose capitulum, and pappus basally connate in a ring.

The section *Anastraphioides* also appears as a monophyletic group in the analysis (Fig. 1), more related to *Richterago* than other species of *Gochnatia* as that genus is currently defined. The characters that distinguish the species of the section *Anastraphioides* from those of other sections of *Gochnatia* include: coriaceous and spinose-dentate leaves in the majority of taxa; anthers with acuminate apical appendages and anther tails usually smooth or short laciniate; and pappus of the achenes with bristles of uniform length and thickness (Type A), usually in a single series and either free or joined at the base.

The presence of pappus bristles in a single series, anthers inserted below the throat of the corolla, and leaves with spiny dentate margins are the diagnostic characters with which D. DON (1830) defined the genus *Anastraphia*. The traditional definition of the genus *Gochnatia* (KUNTH 1819) included the character of pappus bristles in two series, in contrast with features of the sections *Anastraphioides* and *Richterago*. Indeed, the nature of the pappus is a key character that reinforces the differences between *Anastraphioides* and *Richterago* on the one hand, with Type A pappus, and the other sections of *Gochnatia* plus related genera on the other hand.

The unique set of characters that separates the current section *Anastraphioides* of the genus *Gochnatia* from related taxa, added to the recognition of the genus *Anastraphia* by D. DON (1830), suggests that a resurrection of the genus *Anastraphia* may be in order. This suggestion is followed up in related works (VENTOSA & HERRERA 2011a, b).

Conclusions

The current section *Anastraphioides* of the genus *Gochnatia* is a monophyletic group more closely related to *Richterago* than to other sections of *Gochnatia*. The characteristics of the pappus reinforce this relationship and distinguish the current section *Anastraphioides* from the other sections of *Gochnatia*, along with characters of leaves, capitula, and flowers. This section makes up a natural group that apparently evolved in the Antilles, principally Cuba, from a common ancestor shared with *Richterago*, a genus with Brazilian origin. The results suggest that the genus *Anastraphia* should be resurrected for the species currently in the section *Anastraphioides*. They further suggest that the other sections currently included in the genus *Gochnatia* be thoroughly reviewed, especially the section *Hedraiophyllum*, which may end up being considered as another genus independent of *Gochnatia* and related to *Cyclolepis*.

Acknowledgements

We thank Drs. GISELA SANCHO and MARÍA CRISTINA TELLERÍA of the Natural History Museum of La Plata, Argentina, for their helpful suggestions regarding this analysis. The Red Latinoamericana de Botánica (Latin American Botanical Network) supported the first author's work in Argentina. PETER FEINSINGER helped with the English translation.

References

- BREMER, K. 1994. *Asteraceae: Cladistics & Classification*. Timber Press, Portland, USA.
- CABRERA, A. 1971. Revisión del género *Gochnatia* (Compositae). *Revista de Museo de La Plata*, Sección Botánica, n.s. 12: 1–160.
- DE CANDOLLE, A. P. 1836. *Prodromus Systematis Naturalis Regni Vegetabilis*, vol. 5. Treuttel & Würtz, Paris.
- DON, D. 1830. Descriptions of the new genera and species of the class Compositae belonging to the floras of Peru, Mexico, and Chile. *Trans. Linn. Soc.* xvi: 169–303.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 786–791.
- FREIRE, S.E., KATINAS, L. & G. SANCHO 2002. *Gochnatia* (Asteraceae: Mutisieae) and the *Gochnatia* complex: Taxonomic implications from morphology. *Ann. Missouri Bot. Gard.* 89: 524–550.
- GOLOBOFF, P., FARRIS, J. & K. NIXON 2003. TNT: tree analysis using new technology. <http://www.zmuc.dk/public/phylogeny>.
- HIND, D. J. H. 2007. Tribe Mutisieae. Pp. 90–123 In: K. KUBITZKI (ed.), *The Families and Genera of Vascular Plants*, Vol 8. Springer, Berlin and Heidelberg.
- HOLMGREN, P. K., HOLMGREN, N. H. & L. C. BARNETT 1990. *Index Herbariorum*. Part I: The Herbaria of the world. Eighth edition. International Association for Plant Taxonomy. New York Botanical Garden, Bronx, New York.
- JERVIS, R. N. 1954. *A Summary of the Genus Gochnatia*. Including a revision of the West Indies Species which comprise the section *Anastraphioideae*. Ph D. Dissertation, University of Michigan.
- KATINAS, L., PRUSKI, J., SANCHO, G. & M. C. TELLERIA 2008. The subfamily Mutisioideae (Asteraceae). *Botanical Review* 74: 469–716.
- KUNTH, K. 1819. In: HUMBOLDT, F. H. A. VON, BONPLAND, A. J. & C. S. KUNTH, *Nova Genera et Species plantarum*, iv. 19. t. 309.
- LESSING, C. F. 1830. De Synanthereis herbarii regii Berolinensis dissertatio secunda. *Linnaea* 5: 1–42.
- NIXON, K. C. 1999. Winclada ver. 0.9.99+ (BETA). Preliminary documentation.

- PANERO, J. L. & V. A. FUNK 2002. Toward a phylogenetic subfamilial classification for the Compositae (Asteraceae). *Proceedings of the Biological Society of Washington* 115: 909–922.
- PANERO, J. L. & V. A. FUNK 2008. The value of sampling anomalous taxa in phylogenetic studies: Major clades of the Asteraceae revealed. *Molecular Phylogenetics and Evolution* 47: 757–782.
- ROQUE, N. & J. R. PIRANI 2001. Reinstatement of the name *Richtera* KUNTZE and recircumscription of the genus to include species formerly treated as *Actinoseris* (ENDL.) CABRERA (Compositae, Mutisieae). *Taxon* 50: 1155–1160.
- ROQUE, N. & M. S. F. SILVESTRE-CAPELATO 2001. Generic delimitation of *Gochnatia*, *Richtera* and *Ianthopappus* (Compositae-Mutisieae) based on pollen morphology. *Grana Palynologica* 40: 197–204.
- ROQUE, N. 2001. Five new species of *Richtera* (Compositae, Mutisieae): A genus endemic to Brazil. *Novon* 11: 341–349.
- SANCHO, G. 2000. Revisión y filogenia de la sección *Moquiniastrium* CABRERA del género *Gochnatia* KUNTH (Asteraceae, Mutisieae). *Fontqueria* 54: 61–122.
- SANCHO, G. & S. FREIRE 2009. The tribes Gochnatieae and Hyalideae. Pp. 249–260 In: FUNK, V. A., SUSANNA, A., STUESSY, T. F. & R. J. BAYER (eds.), *Systematics, evolution, and biogeography of Compositae*. IAPT, Vienna.
- SANCHO, G., FREIRE, S. E., KATINAS, L. & M. C. TELLERÍA 2005. A new species and a new combination in Andean Mutisieae (Asteraceae). *Taxon* 54: 85–90.
- VENTOSA RODRIGUEZ, I. & P. HERRERA OLIVER 2011a. Restoration of the name *Anaethaphia* to define the species in the section *Anaethaphioides* of *Gochnatia* (Gochnatioideae, Asteraceae). *Comp. Newsl.* 49: 23–37.
- VENTOSA RODRIGUEZ, I. & P. HERRERA OLIVER 2011b. Five new species of *Anaethaphia* D. DON (Gochnatioideae, Asteraceae) from Cuba. *Comp. Newsl.* 49: 38–35.



Fig. 1. Cladogram of strict consensus of the 24 most parsimonious trees resulting from the phylogenetic analysis of morphological, anatomical and palynological data of 46 species. Length = 201 steps, consistency index (CI) = 0,28 and retention index (RI) = 0,60. Vertical lines at the right define the sections of the genus *Gochnatia* as discussed in the text. Bootstrap values are presented above nodes.

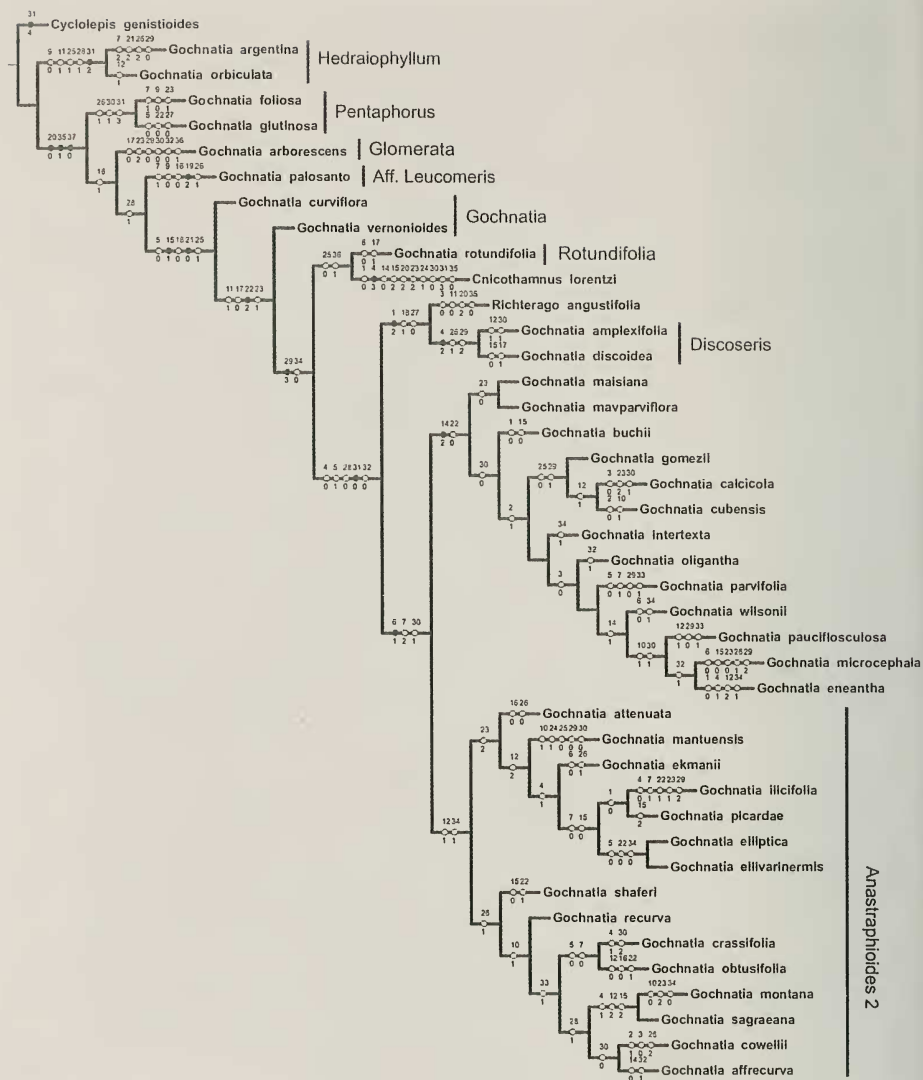


Fig. 2. One of the 24 most parsimonious trees (AMP) resulting from the phylogenetic analysis of morphological, anatomical and palynological data of 46 species (L= 201, CI= 0,28, RI= 0,60). Vertical lines at the right define the sections of the genus *Gochnatia* as discussed in the text. Numbers above branches represent characters (see Table 1), numbers below branches represent states of characters. Black circles represent synapomorphies, white (open) circles homoplasies.